# Post-settlement effects of habitat type and predator size on cannibalism of glaucothoe and juveniles of red king crab *Paralithodes camtschaticus*

Bradley G. Stevens[*], Katherine M. Swiney

*National Marine Fisheries Service, Alaska Fisheries Science Center, Kodiak Fisheries Research Center, 301 Research Ct.,*
*Kodiak, AK 99615, United States*

## Abstract

Postlarval (glaucothoe) and juvenile (first crab stage, C1) red king crab *Paralithodes camtschaticus* actively select structurally complex substrata for settlement. Such habitats may provide them with shelter from predation during critical early stages. We tested this hypothesis by placing glaucothoe and juvenile crab in aquaria with or without natural or artificial habitats, and with or without predators (1–3-year-old red king crab) of two different sizes. Predators caused increased mortality of glaucothoe, but predator size, habitat presence and habitat type had no effect on survival. Predators caused significant mortality of C1 crabs in the absence of habitat, and mortality was inversely related to predator size. Density of glaucothoe on habitats was similar with or without predators, but density of C1 crab on habitats was higher than that of glaucothoe, and increased in the presence of large predators. Active selection for complex substrata by settling glaucothoe does not reduce cannibalism, but may pre-position them for improved survival after metamorphosis. In contrast, juvenile crabs modify their behavior to achieve higher densities in refuge habitats, which tends to dampen the effect of predation. These survival strategies may have evolved to compensate for the greater risk of predation in open habitats.
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## 1. Introduction

For most decapod crustaceans, the transition from planktonic larva to benthic juvenile occurs during the megalopa stage (Jensen, 1989; Eggleston and Armstrong, 1995; Welch et al., 1997; Forward et al., 2001). Changes in activity level (from swimming to sedentary), body form, habitat, diet, predation risk, and energetics make this stage one of the most vulnerable in the life of the animal, and prone to high mortality (Fernandez et al., 1993; Eggleston and Armstrong, 1995). Because the environmental con-

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* Corresponding author. Tel.: +1 907 481 1726.
  *E-mail address:* bradley.g.stevens@noaa.gov (B.G. Stevens).

ditions required for this process to occur are often restricted, it can be considered a critical bottleneck through which individuals must pass (Wahle and Steneck, 1991). Knowledge about the settlement process could allow understanding of how survival and year-class strength are influenced by environment, and is important for the development of aquaculture or stock enhancement schemes for decapod crustaceans.

Many species of decapods are attracted to specific substrata (Forward et al., 2001), and structurally complex habitats are particularly important. For example, Dungeness crab *Cancer magister* settle preferentially in complex shell habitats at much higher densities than on surrounding open mud (Fernandez et al., 1993). Concentration of juveniles in refuge habitats can lead to competition and cannibalism, and radically alter the size structure and abundance of settling cohorts. In snow crab *Chionoecetes opilio*, competition may result in lethal or sublethal effects such as reduced growth, delayed molting, and increased limb loss (Sainte-Marie and Lafrance, 2002). In eastern Canada, snow crabs exhibit unstable annual recruitment and alternating periods of weak and strong year classes, with a period lasting about 8 years. Such large-scale cycles of abundance could be the result of cannibalism, competition between newly settled juvenile crabs and earlier settlers or previous cohorts (Sainte-Marie et al., 1996).

The red king crab (RKC), *Paralithodes camtschaticus*, is a commercially valuable anomuran crab found in the North Pacific Ocean and the Barents Sea (by introduction). In Alaska, peak landings of 82,000 t occurred in 1980, but declined to 7950 t in 1982, and populations have remained at low levels since. Recruitment of some North Pacific crab species has been linked to environmental factors including wind stress (Rosenkranz et al., 2001) and decadal cycles of temperature (Zheng and Kruse, 2000), but direct relationships between survival of king crabs and environmental variables have not yet been demonstrated. Juvenile king crabs <2 years old (yo) have only been found in complex habitats consisting of hydroids and mussel beds (Sundberg and Clausen, 1977), bryozoans, polychaete tube reefs, and similar biogenic structures (Dew, 1990; Loher and Armstrong, 2000). Laboratory studies on settling behavior have shown that the transitional settling stage, called a

glaucothoe in anomuran crabs (Marukawa, 1933; Haynes, 1982), actively selects structurally complex habitats resembling those they occupy in nature, and actively avoids settlement on open sand (Stevens and Kittaka, 1998; Stevens, 2003). If suitable habitat is available, glaucothoe will settle within hours; otherwise, they will continue swimming until metamorphosis. Unlike brachyuran megalopae, red king crab glaucothoe are non-feeding (Stevens and Kittaka, 1998).

Obligatory settlement in structurally complex habitats is usually associated with refuge from predation. Therefore, we conducted a laboratory study to determine the effect of refuge habitats and predators (1 yo and 3 yo crab) on the short-term, post-settlement survival and behavior of glaucothoe and first stage juvenile crab (C1). Our experiments utilized both natural and artificial habitats and were conducted over 24-h intervals. In addition, we conducted a-posteriori tests to determine if predators affected the behavior of settlers (as evidenced by their position on or off the refuge habitats).

## 2. Materials and methods

### 2.1. Crab cultivation

Mature female RKC were collected by scuba divers in December 2001 and maintained at the Kodiak Fisheries Research Center on a mixed diet of fish and squid until their larvae hatched. After hatching started, individual females were placed in 50-L plastic tubs containing filtered seawater and an airstone. Tubs were placed in a 2500-L fiberglass tank containing flowing ambient temperature seawater and left overnight. The next morning, 2000 stage I zoea larvae were collected in a beaker and equally distributed to four 20-L culture containers with filtered seawater, at a density of 25 per liter and maintained at 8 °C. Larvae were fed ad libitum on a diet of 18–24 h old *Artemia salina* nauplii daily and were transferred to new tanks with clean filtered seawater weekly. Because of the protracted nature of hatching and development (author's unpublished data), it was not possible to expect production of 1500 glaucothoe on the same date, or even the same week. Furthermore, failure of a single mass culture

would have jeopardized the entire series of experiments. Additionally, it was not possible to produce glaucothoe and C1 stages simultaneously. For these reasons, we cultivated three separate batches of king crab larvae. These were collected for cultivation at weekly intervals, starting on 28 February (batch 1), 7 March (batch 2) and 13 March 2002 (batch 3). Larvae passed through four zoeal stages and metamorphosed to glaucothoe after about 1 month. Survival from hatching to the glaucothoe stage was 35%, 48%, and 47% in batches 1, 2, and 3, respectively.

## 2.2. Experimental apparatus

Five experiments were conducted: three using glaucothoe (G) and two using first instar (stage C1) juvenile crab. The experimental protocol for all experiments was identical, as follows. Twelve 12-L plastic aquaria ("tanks") were immersed in a water bath with ambient temperature seawater flowing around them. The bottom of each tank ($18 \times 31$ cm) was covered with a 2-cm layer of beach sand that had been washed in fresh water, dried at room temperature, and rinsed in saltwater three times to remove the finest particles. Sand was sieved to determine size ranges; 99% was <0.6 mm, with the remainder between 0.6 and 1.4 mm. Each tank contained 10 l of filtered seawater, with an airstone ($1 \times 1 \times 3$ cm) at one end. The 12 tanks were divided into 3 treatment groups, designated as NP (no predator), SP (small predator), or LP (large predator), with 4 replicates each. Tanks were arranged in a systematic alternating order, so that each experimental group was equally distributed around the water bath. The water bath was covered with a sheet of translucent green plastic to reduce light levels to <5 lx during daytime. Subdued natural lighting came from partially shuttered glass windows 2 m away and parallel to the long axis of the water bath, supplemented by overhead fluorescent lighting during daytime.

## 2.3. Glaucothoe habitat/predation experiments

The first three experiments were conducted with glaucothoe. The first experiment used no habitats other than the sand substratum, the second used artificial habitats, and the third used natural habitats. All experiments used the same procedures.

### 2.3.1. Experiment G1: glaucothoe on sand substratum

All 12 tanks had no habitat other than the sand substratum and airstone. Three hundred glaucothoe from batch 1 (28 February) were collected on 3 April (all within 3 days after metamorphosis) from the four culture containers. After mixing together randomly, 25 glaucothoe were placed into each of twelve 100 ml plastic beakers that were floated in the experimental tanks in order to allow equilibration from the 8 °C culture temperature to the ambient temperature in the tanks (about 5 °C). Glaucothoe were released after 1 h and allowed to acclimate in the tanks for 24 h. Introduction times were staggered by 1 h to allow time for counting the glaucothoe at the end of the experiment, so that glaucothoe were introduced into each of the four NP tanks at 9:00, into the SP tanks at 10:00, and into the LP tanks at 11:00.

The following day, predators were introduced into the SP and LP tanks at 10:00 and 11:00, respectively. The four SP tanks each received two 1 yo king crab (mean carapace length, CL, $14.1 \pm 0.2$ mm S.D.), and each of the LP tanks received a single 3 yo king crab (mean CL $40.0 \pm 2.3$ mm S.D.). The plastic cover was then replaced. NP tanks did not receive predators. All predators had been cultivated from larvae in the laboratory and fed ad libitum on squid, fish, and pelleted foods. Predators were randomly assigned to tanks within their treatment group. The same individual predators were used in all subsequent experiments in order to eliminate any differences in predation rates. Predators were not fed for at least 48 h prior to, or during the experimental periods.

On the third day, the plastic tank cover was removed at 9:00 and the number of swimming glaucothoe were immediately counted in all 12 tanks (this was not done in a time-staggered manner because removal of the cover affected behavior in all tanks). The 4 tanks in each experimental group were then removed, and all glaucothoe were recovered and counted. Counting required about 15 min per tank (1 h per treatment group), and it was not possible to count all tanks simultaneously. Therefore, recovery of each group was staggered as before so that NP tanks were removed for counting at 9:00, SP tanks at 10:00, and LP tanks at 11:00. Although the time of day at which counting occurred differed slightly between treatments, this procedure insured that the predators were in each tank for a complete 24 h cycle.

Furthermore, we avoided counting during periods of greatest activity, thereby minimizing the impact of slightly different counting times on behavior. Prior to removing the tanks from the water bath, any glaucothoe on the airstones were counted. The predators were then removed, and all remaining glaucothoe were collected with a large-bore pipette and counted. Live glaucothoe were recorded in three locations: swimming, on the sand substratum, or on the airstone. Moribund glaucothoe were examined under a microscope and declared dead if they exhibited swelling, discoloration, and absence of heartbeats.

In order to test our recovery methods, sand from three tanks was rinsed through a 1.4 mm sieve after removal of all visible glaucothoe from the tank. No additional glaucothoe were recovered by this method. We concluded that glaucothoe did not burrow in sand, and 100% recovery could be achieved by surface examination.

### 2.3.2. Experiment G2: glaucothoe with artificial habitats

For this experiment, artificial habitats were constructed from green plastic kitchen scrubbers that were cut it in half, wrapped around a small rock (for weight), and secured with plastic cable ties. All habitats were rinsed in running warm tap water for 24 h prior to use, and then placed into the experimental tanks with new filtered seawater on 8 April and allowed to soak for 48 h. Each tank received a single habitat, approximately $9 \times 7.5 \times 5$ cm, that covered 12.5% of the tank bottom, and was large enough to accommodate all glaucothoe or juvenile crabs. Glaucothoe were collected from batch 2 on 10 April, so that all were the same post-hatch age as those used for the previous experiment, i.e., all were within 1–3 days of metamorphosis. Again, 25 individuals were placed into each tank at staggered times as before and allowed to acclimate for 24 h. On 11 April, predators were introduced at staggered times to the same SP or LP tanks as before and allowed to remain in the tanks for 24 h. On 12 April, the tank cover was removed, swimmers were counted, and glaucothoe collected, as before. Habitats (excluding sand) were removed and examined systematically, and surviving glaucothoe removed and counted; we did not distinguish between survivors found on the

outside or inside of the habitats, as those locations were not clearly definable. Surviving glaucothoe were recorded in four locations; swimming, sand, airstones or habitats. Proportions on airstones never exceeded 21% of total survivors in any experiment, so for analytical purposes, the latter two categories were combined.

### 2.3.3. Experiment G3: glaucothoe with natural habitats

For this experiment, each tank received 3.5–4.0 g of the branched red alga *Odonthalia floccosa*, similar in areal extent to the artificial habitats previously described, i.e., covering 10–15% of the tank bottom. Similar branched algae (*Neorhodomela larix*) were a preferred substratum in prior experiments (Stevens, 2003). New seawater and algae were placed into the tanks on 15 April, 25 glaucothoe were collected from batch 3 and introduced to each tank on 16 April, predators were introduced on 17 April, and all glaucothoe were removed and counted on 18 April.

### 2.4. Juvenile crab habitat/predation experiments

Two experiments were conducted with first instar juvenile crab (stage C1). The first experiment used no habitats other than the bare sand substratum, and the second used artificial habitats. There were not enough C1 crab of known age remaining to conduct a third experiment using algae. All experiments used the same apparatus and procedures as those for the glaucothoe experiments. All C1 crab had metamorphosed from glaucothoe that were not used in the previous experiments, but belonged to the same hatching groups (i.e., glaucothoe from batch 1 that were not used in experiment G1 (above) and later molted to juvenile crab were used in experiment J1). This ensured that experiments conducted in successive weeks utilized crab that were all the same age post-metamorphosis.

### 2.4.1. Experiment J1: juvenile crab on sand substratum

On 29 April, 20 juvenile (C1) crab from batch 1 were introduced into each of 4 tanks in the NP group at 09:00, into the SP tanks at 10:00, and into the LP tanks at 11:00. After 24 h, two 1 yo king crab were placed into each of the four SP tanks; LP tanks

received a single 3 yo king crab. The next day, predators were removed, and live C1 crabs were recorded as being on the sand or airstone. In this experiment, predator conditions differed in both size and number because it represented a more natural situation, in which 1 yo crab would outnumber 3 yo crab at any given time or location due to natural mortality. In addition, the experimental tanks would not accommodate two 3 yo crabs without conflict between them. Furthermore, it was not our goal to evaluate predation per capita, but rather to gauge the effectiveness of habitats under different predator conditions which naturally incorporate changes in both size and number of predators.

### 2.4.2. Experiment J2: juvenile crab with artificial habitats

The following week (6 May) the experiment was repeated using C1 crab from batch 2 and artificial habitats. However, only 19 crab were available for placement into each tank. Surviving C1 crab were recorded as being on the sand, habitats, or airstone.

### 2.5. Analysis

Analysis was conducted separately for glaucothoe and juvenile crab. Three questions of primary interest were formed as null hypotheses:

**H01.** There is no difference in survival due to the presence/absence of predators.

**H02.** There is no difference in survival between tanks with different types of habitats.

**H03.** There is no difference in survival due to predator conditions. However, we did not attempt to separate the effects of size or number of predators.

For these questions, the proportion of crab surviving in four replicates was compared between treatments, after angular transformation (Zar, 1984). For glaucothoe, a two-factor ANOVA was conducted across three habitat conditions (none, i.e., sand, artificial, or natural), three predator conditions (none, small, large), and their two-way interactions; a total of 36 samples (four replicates in each treatment) were used. Juvenile crab data consisted of 24 samples because only two habitat types were used. Post-hoc tests were conducted using Tukey's HSD test, if the F-

tests were significant, and values of $P<0.05$ were considered significant (Zar, 1984). Error variances were compared using Levene's test.

A fourth, post-hoc hypothesis was formulated after completion of the experiments:

**H04.** There is no difference in numbers of surviving crab on the habitats due to the presence or absence of predators (i.e., the presence of predators did not affect the behavior of crab, manifested as altered density on the habitats).

Hypothesis 4 is more difficult to test because it was developed a-posteriori and the experiment was not designed specifically to address it. A definitive answer would require separation of the effects of predation and behavior, which are confounded in the present experiments. However, by comparing both the proportion and number of crab on refuge habitats between experiments with and without predators, some inferences can be drawn. Numbers of crab recovered from refuge habitats were compared using the log-likelihood ratio ($G$). For glaucothoe a $2\times3$ contingency table was used, comparing two habitat types (artificial or algae) and three predator conditions (none, small, large), whereas for juvenile crab, only one (artificial) habitat type was used. Proportions of surviving crab on refuge habitats were also compared between predator conditions using a one-way ANOVA, after angular transformation; for glaucothoe, both habitat types (artificial and algae) were combined. Statistics were conducted using SPSS procedure Oneway, or SAS procedure ANOVA. Mean values $\pm 1$ standard deviation (S.D.) are given where appropriate.

## 3. Results

### 3.1. Experiments with glaucothoe

All glaucothoe, including the few that died, were recovered from the tanks with no predators. The error variances of survival were non-homogeneous ($F=4.475$, $P<0.01$), however, ANOVA is robust to departures from normality and homogeneity, especially if the sample sizes are similar (Zar, 1984). Predators caused significantly reduced survival of glaucothoe (ANOVA, $F=87.4$, $P<0.001$; Table 1), so

Table 1
Two-factor ANOVA of survival of *P. camtschaticus* glaucothoe in experiments G1, G2, and G3 with different habitat and predator conditions (after angular-transformation)

| Source | df | MS | F | P |
|---|---|---|---|---|
| Corrected model | 8 | 4342.3 | 22.449 | <0.001 |
| Intercept | 1 | 49,433.9 | 255.568 | <0.001 |
| Habitats | 2 | 133.2 | 0.688 | 0.511 |
| Predators | 2 | 16,905.5 | 87.400 | <0.001 |
| Hab×Pred | 4 | 165.3 | 0.855 | 0.503 |
| Error | 27 | 193.4 | | |
| Total | 36 | | | |

Table 2
Mean percent survival ($\pm 1$ S.D.) of postlarval (glaucothoe) and juvenile (C1) *P. camtschaticus* in tanks with different substrata and predator sizes

| | | Glaucothoe | Juveniles (C1) |
|---|---|---|---|
| Predator size | None | 95.7±4.0 a | 99.3±1.9 d |
| | Small | 8.0±6.8 b | 18.4±23.4 e |
| | Large | 16.7±22.5 b | 43.2±38.1 f |
| Habitat type | Sand | 38.3±47.6 c | 37.1±47.2 g |
| | Artificial | 40.0±41.3 c | 70.2±30.9 h |
| | Algae | 42.0±41.1 c | nd |

Tukey's HSD was calculated on angular transformed proportions; letters indicate groups with similar mean survival. nd, no data.

$H_{01}$ was rejected. Mean survival in tanks with no predators (95.7±4.0%) was significantly greater than in tanks with two small predators (8.0±6.8%) or a single large predator (16.7±22.5%, Fig. 1; HSD test, Table 2). Habitat type (none, artificial, or algae) had no significant effect (ANOVA, $F=0.688$, $P=0.511$), although the power of the test was low (0.158); survival of glaucothoe was similar with or without artificial or natural habitats, so $H_{02}$ was not rejected. Predator conditions also had no effect because survival in the presence of small or large predators was not significantly different (Fig. 1, Table 2), so $H_{03}$ was not rejected. Thus, access to refuge habitats did not significantly improve survival of glaucothoe, even in the presence of predators.

Small predators consumed almost 100% of glaucothoe in the tanks with bare sand (Fig. 1). Although the interaction effect between habitats and predators was not significant, it may have been obscured by

inclusion of experiment G1 with no predators (and subsequently high survival). Contingency table analysis on numbers of surviving crab from experiments G2 and G3 (small and large predators, respectively) with three habitat conditions, was significant ($G=8.835$, $df=2$, $P<0.025$; Table 3A), indicating that small predators were more efficient than large predators in tanks with no habitats other than sand.

There was no significant difference in the numbers of glaucothoe present on habitats (Fig. 2) in tanks with or without predators of different sizes ($G=0.294$, $df=2$, $P>0.05$; Table 3B). The mean density was 4.4±4.3 individuals per habitat. After testing equality of variances ($F=0.65$, $P=0.5349$), the proportions of glaucothoe on refuge habitats (experiments G2 and G3 combined) were compared by ANOVA, and found to be significantly greater ($F=7.043$, $p=0.006$) in the presence of both large and small predators than without predators (HSD test). Therefore, $H_{04}$ was
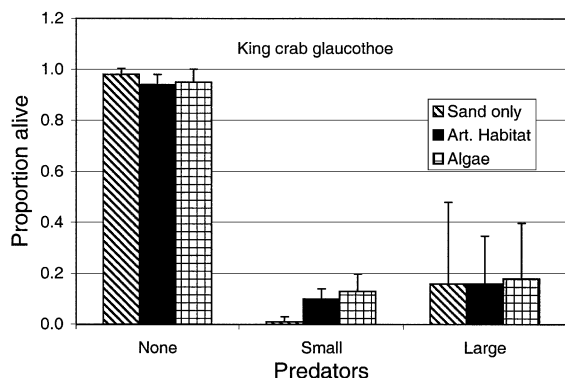


Fig. 1. Proportion of king crab *P. camtschaticus* glaucothoe surviving in different combinations of habitat type and predator conditions (experiments G1, G2, and G3). Error bar represents 1 S.D. See Table 2 for overall means.
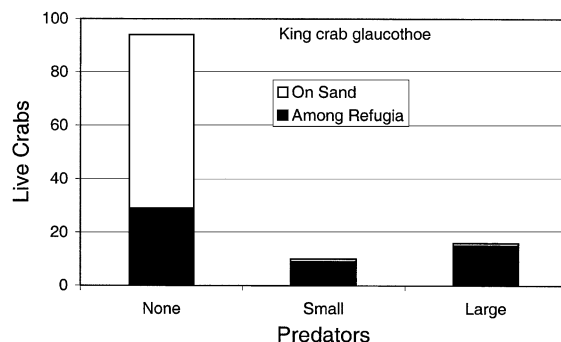


Fig. 2. Number of live king crab *P. camtschaticus* glaucothoe on sand or refugia (shelter and airstones) after 24 h (experiments G1, G2, and G3). There was no significant difference in numbers on refugia between predator conditions.

Table 3A

Numbers of surviving *P. camtschaticus* glaucothoe in tanks with predators (small vs. large), and three habitat conditions (none, artificial, or algae)

| Predators | Habitats | | | Row totals |
|---|---|---|---|---|
| | Sand | Artificial | Algae | |
| Small | 1 (6) | 10 (8) | 13 (10) | 24 |
| Large | 16 (11) | 16 (18) | 18 (21) | 50 |
| Column totals | 17 | 26 | 31 | 74 |

All surviving glaucothoe were included regardless of position in tank. Numbers in parentheses are calculated expected values. The *G*-value was significant: $G=8.835$, $df=2$, $P<0.025$. Thus, small predators were more efficient than large predators in tanks with no habitats.

not rejected. These results imply that the behavior of glaucothoe (manifested as density in the refuge habitat) did not change due to the presence of predators, but the proportion of survivors on refugia increased as a result of predation on errant glaucothoe (those not associated with refuge habitats).

### 3.2. Experiments with juvenile crab

Error variances in the ANOVA were similar ($F=2.255$, $P=0.09$). Survival of C1 crab was significantly affected by habitat type, predator conditions, and the interaction of habitat×predators (Table 4); therefore $H_{01}$, $H_{02}$, and $H_{03}$ were all rejected. Mean survival of C1 crab in tanks with habitats ($70.2\pm30.9\%$) was significantly greater than in tanks
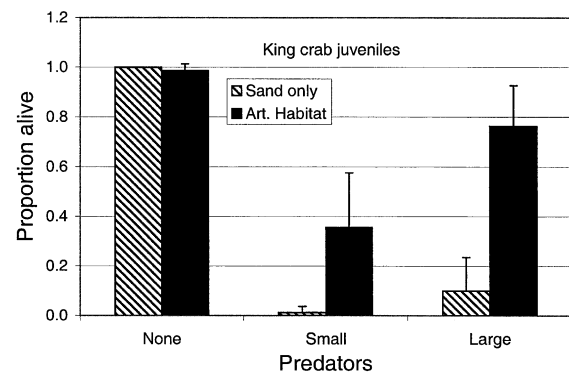


Fig. 3. Proportion of juvenile (stage C1) king crab *P. camtschaticus* surviving in different combinations of habitat type and predator conditions (experiments J1 and J2). Size of predators, and presence/absence of habitats were significant effects. Smaller 1 yo king crabs were more effective predators than larger 3 yo crabs, and both were more effective in the absence of shelters.

Table 3B

Numbers of *P. camtschaticus* glaucothoe from refugia (habitats or airstones) in tanks with or without predators of two sizes

| Habitats | Predators | | | Row totals |
|---|---|---|---|---|
| | None | Small | Large | |
| Artificial | 14 (15) | 9 (9) | 11 (10) | 34 |
| Algae | 22 (21) | 12 (12) | 13 (14) | 47 |
| Column totals | 36 | 21 | 24 | 81 |

The *G*-value was not significant: $G=0.294$, $df=2$, $P>0.05$. Thus, the presence of predators did not affect the number of glaucothoe occupying habitats.

without habitats other than sand ($37.1\pm47.2\%$; Table 2, Fig. 3). Survival in tanks without predators ($99.3\pm1.9\%$) was significantly greater than in those with a single large predator ($43.2\pm38.1\%$), or two small predators ($18.4\pm23.4\%$); both the presence and type of predators had significant effects (Table 2, Fig. 4).

Considering only experiment J2, and after comparing variances ($F=2.58$, $P=0.1302$), a significantly greater proportion of surviving crab were on the habitats in tanks with predators (100%, Fig. 4), than in tanks without predators (47%) ($F=199.9$, $P<0.001$). The number of crabs on refuge habitats did not differ between treatments with none or small predators (mean density $8.8\pm2.2$ crabs per habitat versus $6.8\pm4.2$, respectively), but increased significantly to a mean of $14.5\pm3.1$ in the presence of large predators ($G=12.53$, $df=2$, $P<0.005$). Therefore $H_{04}$ was also rejected. Furthermore, densities of juvenile crab on the habitats (overall mean $10.0\pm4.5$) were more than twice those achieved by glaucothoe (overall mean $4.4\pm4.3$). These results imply that juvenile crab achieve increased densities

Table 4

Two-factor ANOVA of survival of juvenile *P. camtschaticus* in experiments J1 and J2 with different habitat and predator conditions, after angular transformation

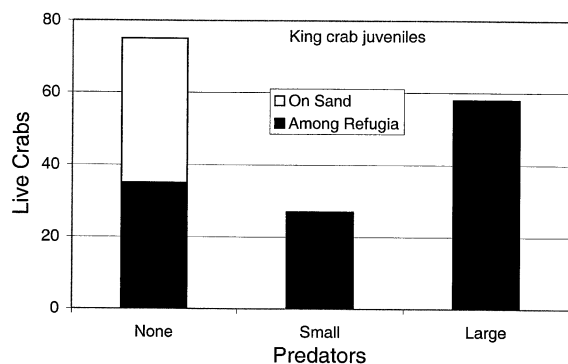| Source | df | MS | F | P |
|---|---|---|---|---|
| Corrected model | 5 | 5414.7 | 43.548 | <0.001 |
| Intercept | 1 | 58,128.1 | 467.497 | <0.001 |
| Habitats | 1 | 4191.9 | 33.714 | <0.001 |
| Predators | 2 | 9974.8 | 80.222 | <0.001 |
| Hab×Pred | 2 | 1466.0 | 11.79 | 0.001 |
| Error | 18 | 1274.3 | | |
| Total | 24 | | | |

Fig. 4. Number of live juvenile (stage C1) king crab *P. camtschaticus* on sand or refugia (shelter and airstones) after 24 h (experiment J2). In tanks with predators, all surviving juvenile crabs were located on refugia. Density of juvenile crabs on refugia was greater when large predators were present.

as a result of migration onto the refuge habitats to avoid predation by large crabs, which preyed mostly on errant juveniles.

## 4. Discussion

Red king crab glaucothoe actively settle on complex substrata, whether live or artificial, similar to that on which 1 yo crab are found in nature (Stevens and Kittaka, 1998; Stevens, 2003). We expected that such selectivity would result in improved survival. However, our experiments show that such behavior does not provide much protection for glaucothoe from older conspecifics that cohabitate in, and can forage effectively among, such habitats. In our experiments, both 1 yo and 3 yo crab were effective predators on glaucothoe, and to a lesser degree on C1 crab. In contrast to C1 crab, glaucothoe are active daytime swimmers but settled and became inactive at night, even on undesirable substrata such as sand (Stevens and Kittaka, 1998). Such variable activity levels may render glaucothoe more susceptible to predation than C1 crabs under these experimental conditions.

Although settlement on refugia did not protect glaucothoe from intraspecific predation, it did improve survival of C1 crab by a factor of 2. Furthermore, compared to 1 yo crab, larger 3 yo crab were less effective predators on C1 crab. This effect was probably not due to the number of predators

(two small crab vs. one larger crab), because it did not occur for glaucothoe. One possible explanation is that the morphology of the chelipeds may restrict the size of prey that can be efficiently captured and handled. We have observed that 3 yo king crab can effectively handle chunks of food about 1 cm in size, but have much more difficulty handling food pellets that are <3 mm diameter (B. Stevens, unpublished data). Glaucothoe may be more easily preyed on by 1 yo crab than by 3 yo crab because the chelipeds of the former are closer to the size of the prey, whereas those of the latter are much larger. This mechanism may be the reason that grass shrimp (*Palaemonetes* sp.) are more efficient predators of mud crab *Panopeus herbstii* megalopae than are juvenile blue crab, *Callinectes sapidus* (Dittel et al., 1996). Furthermore, larger predators need larger prey to provide them with more nutrition "per bite" relative to the amount of energy spent foraging. For example, juvenile blue crab *C. sapidus* selectively prey on snails with thinner shells that require less handling time relative to their caloric value, in accordance with a theoretical cost/benefit ratio (Cote et al., 2001).

Stage C1 RKC also exhibited behavioral differences from glaucothoe by achieving greater habitat-specific densities. In our experiment, densities of glaucothoe on the habitats were low and did not change in the presence of predators, whereas densities of C1 crab were greater and increased by a factor of 2 in the presence of large (3 yo) predators, although not in the presence of small (1 yo) predators. These data support the idea that the carrying capacity of natural habitats may be controlled by predation and cannibalism, as has been demonstrated for settling blue crab (Heck et al., 2001). Virtually 100% of settling glaucothoe were consumed by 1 yo crab in the absence of complex refuge habitat and 90% were consumed when habitat was present, as were up to 65% of stage C1 juvenile king crab. Under these conditions, all surviving C1 crab occurred among refugia and all errant settlers were consumed.

Our data show that juvenile RKC are capable of inflicting severe mortality to settling year classes via cannibalism. Demonstrated levels of 24-h cannibalism probably differ from naturally occurring levels due to the density of settlers, lack of alternative

prey, and inexperience with predation. For example, predation by juvenile Japanese flounder *Paralichthys olivaceus* on "naive" sandy shore crab *Matuta lunaris* was higher than on "experienced" prey (Hossain et al., 2002). Cannibalism rates may also have been influenced by diet; juvenile king crab fed a low-growth diet (shrimp tails) exhibited significantly higher rates of cannibalism than those fed a high-growth diet such as mussels (Broderson et al., 1989). Studies with other species of crab have shown that cannibalism is a process that occurs primarily between cohorts or instars rather than among crabs of similar sizes. In snow crab, cannibalism is exerted by older, larger crab on smaller ones, but not among crab of the same size (Sainte-Marie and Lafrance, 2002). When three size classes (settlers, juveniles, adults) of the shore crabs *Chasmagnathus granulata* and *Cyrtograpsus angulatus* were held together, predation on settlers decreased due to predation by adults on juveniles (Luppi et al., 2001). Virtually all cannibalism occurred across cohorts, and essentially none occurred among the settlers themselves, similar to the situation for snow crab.

Most decapod species studied to date benefit from availability of shelter habitats during their early life history. Both megalopae and early stage juveniles of the Dungeness crab *C. magister* seek refuge among intertidal bivalve shells where predation by fish, birds, and larger conspecifics is much lower, although intra-cohort cannibalism is higher in this habitat (Fernandez et al., 1993; McDonald et al., 2001). In the presence of fish or crustacean predators, megalopae of the mud crab *P. herbstii* have better survival among shell rubble than on sand, seaweed, or marsh grass (Dittel et al., 1996). Postlarval and juvenile spiny lobster settle preferentially among branched red algae (Herrnkind and Butler, 1986), and will also settle among artificial habitats (Butler and Herrnkind, 1997). Green shore crab (*Carcinus maenas*) megalopae settled in greater densities among complex habitats such as algae, mussels, and eelgrass (mean 114–232 settlers per m$^2$), than on open sand habitats (4 settlers per m$^2$) (Hedvall et al., 1998; Moksnes, 2002), whereas older conspecifics (crab stages C2 to C9) were concentrated in mussel beds. Moksnes and Wennhage (2001) suggested that complex substrata may be only transitional habitats for postlarvae, which later redistribute themselves to different habitats by emigration.

Post-settlement redistribution of crab into different habitats may further reduce cannibalism. Stage C1–C2 blue crab remain relatively close to settlement sites in seagrass beds, but stage C3–C5 crab redistribute themselves planktonically by swimming up into the water column when current velocities exceed 10 cm s$^{-2}$ (Blackmon and Eggleston, 2001), such as during storm events (Etherington and Eggleston, 2000). Postlarval spiny lobsters settle initially in macroalgal habitats (Herrnkind and Butler, 1986; Butler and Herrnkind, 1997), and later redistribute themselves into crevice habitats among coral reefs, where they live gregariously (Childress and Herrnkind, 2001). However, rather than improving survival, gregarious den sharing by lobsters is seen as a consequence of orientation toward conspecific odor cues, a behavior that benefits small lobsters by reducing the time that they spend searching for shelter out in the open where predation rates are higher (Childress and Herrnkind, 2001). This "guide effect" thus results in lower mortality *prior* to entering the crevice habitat. Perhaps the shelter-seeking behavior of king crab glaucothoe is a preadaptation for improving survival of later stage crabs.

Both laboratory and field studies show that habitat selection by settling stages is the major process responsible for the distribution of juvenile decapods. Although predation of megalopae should be lower in refuge habitats than in open habitats, the presence of predators probably moderates this benefit. Nonetheless, in our experiments, selection for complex substrata had a greater effect on settler distribution than did predation. Predation, particularly cannibalism, represents a major evolutionary process reinforcing this behavior.

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